

DEMOGRAPHIC STUDY OF THE RARE
CORYPHANTHA ROBBINSORUM (CACTACEAE) IN
SOUTHEASTERN ARIZONA

ROBERT J. SCHMALZEL
Oracle, AZ

FRANK W. REICHENBACHER*
Southwestern Field Biologists
8230 E. Broadway Blvd., Suite W8 Tucson, AZ 85710-4002

SUE RUTMAN
U.S. Fish and Wildlife Service
3616 W. Thomas Rd., Suite 6 Phoenix, AZ 85019

ABSTRACT

Growth, fecundity and demography of the cactus *Coryphantha robbinsorum* are described based on a five year study of three permanent plots in Cochise County, Arizona. Four size stages were recognized: seeds, juveniles ≤ 11 mm diameter (J1), juveniles > 11 mm diameter (J2), and adults (A). Mean numbers of plants per year per meter² were 1.11 in Plots A and C, and 0.70 in Plot B. The number of flowers and fruits produced annually by each adult was determined. The smallest plants to flower (become adults) were 13 mm in diameter. More than half of the plants flowered upon attaining an 18 mm diameter. Large adults produced more flowers and fruits than did small adults. During the five years, over 50% of the fruit produced by the population came from 25 individuals who represented only 23% of the adult population. The average number of fruits produced annually per adult was 1.58 ± 0.89 (mean ± 1 SD). Number of recruits to J1 was negatively correlated with total rainfall during the 12 months preceding the census. Percent survival of J1 individuals was positively correlated with winter rainfall. Neither percent mortality of J2 and adult individuals, nor fruit and flower production were significantly correlated with preceding summer, winter or annual rainfall. This cactus has a survivorship pattern with a high mortality of seeds (0.9999 individuals per year, estimated based on 33 seeds per fruit) and a decreasing mortality for each stage thereafter (J1 juveniles: 0.209; J2 juveniles: 0.054; adults: 0.027, measured). There were differences between the plots in transition and survival rates measured for the various stage classes. The finite rate of increase (λ) ranged from 1.0036 to 1.0941 for the three plots. The average λ for the 3 plots, 1.0464, predicts a doubling time for the population of about 16 years. Elasticity analysis of λ to various demographic parameters shows that, during the early 1990's adult survivorship contributed most (46–87%) to λ , J2 survivorship and the combined contribution of all growth parameters were less important than adult survivorship in their effect on λ , and fecundity and J1 survivorship were least important. A simulation experiment shows that a hypothetical increase to 50 seeds per fruit would change the average λ from 1.046 to 1.098; and a reduction to 6 seeds per fruit would change λ to 1.003. Projection of the matrix model suggests that *C. robbinsorum* is long-lived. At a stable age distribution, the mean age in the J1 stage is

* Reprint requests, comments, and questions to second author.

estimated to be 1.1–2.0 years, the J2 stage to be 3.4–5.1 years, and the adult stage to be about 17 years. The mean age of parents of offspring produced in a stable age distribution, \bar{A} , is 17.05 years.

Demographic studies require long-term monitoring of populations to obtain the information needed to assess the dynamics of a population. In a recent symposium (Sivinski and Lightfoot 1993) on Southwestern rare plants, at least 10 of the 37 papers presented the results of demographic studies. These studies developed many of the estimates of demographic parameters needed for matrix analysis, but only one of these papers (Maschinski and Rutman 1993) included matrix analyses. Matrix analysis of plant populations provides the means for determining estimates of the finite rate of increase of the population (λ) and the relative contribution of each demographic parameter to λ . This study describes the results of 5 years of demographic monitoring and matrix analysis of a population of *Coryphantha robbinsorum* (Earle) A. D. Zimmerman.

Coryphantha robbinsorum is a federally Threatened Species of cactus protected by the Endangered Species Act (Rutman 1992). This plant is restricted to limestone outcrops in an estimated area of 25 km² in the San Bernardino Valley of Cochise County, southeastern Arizona (Phillips and Brian 1982; U.S. Fish and Wildlife Service 1993) and extreme northern Sonora (Lopresti 1984). Zimmerman (personal communication to Phillips and Brian 1982) estimates that there are about 20,000 plants ($\pm 10,000$) of detectable size for this species. The population of *C. robbinsorum* includes plants that are scattered and plants that occur as small, isolated clusters of 100–1000 plants (U. S. Fish and Wildlife Service 1993).

We determine four demographic parameters of the *C. robbinsorum* population: establishment, mortality, growth and reproduction. These demographic parameters are then examined in relation to rainfall. Water is the major limiting factor for vegetative growth in the deserts and the productivity of arid ecosystems is highly correlated with rainfall (Noy-Meir 1973). High annual variation in establishment and growth has been noted in other cacti and succulents (Jordan and Nobel 1979, 1981; Steenbergh and Lowe 1977; Turner 1990; Johnson et al. 1993). We hypothesize that flower and fruit production are positively associated with rainfall, and mortality is negatively associated with rainfall. Also, because small plants are less able to withstand drought, we hypothesize that juveniles experience high mortality in dry years, low mortality in wet years, and that adults should be little affected by annual variation in rainfall.

A simple stage-classified life cycle graph for *Coryphantha robbinsorum* is constructed and from this life cycle graph the corresponding projection matrix (as outlined by Caswell 1986, 1989) is derived. By matrix analysis, we determine the (1) finite population growth

rate (λ), (2) the stable age distribution, and (3) mean age for each life stage of *Coryphantha robbinsorum*. We then use an elasticity matrix (Caswell 1986) to explore the relative contribution to population growth rate made by several biologically relevant parameters. In particular, we simulate alterations in four parameters to explore their effects on population growth: (1) seed bank survivorship, (2) seed to juvenile establishment rate, (3) adult mortality, and (4) fecundity.

METHODS

Plant surveys. Three circular plots, each with a 3 m radius, were established by the U.S. Fish and Wildlife Service in Cochise County, southeastern Arizona. Each plot was marked in the center with an aluminum spike and aluminum tag. Plot A was established in April 1988 at a site on a hill with a northeast exposure and a 10–20% slope. In April 1989, two more plots were established on the same hill at a site with a southwest exposure (Plot B) and at a site on top of the hill (Plot C). In each plot, every individual plant was labeled with an aluminum tag that was secured next to the plant with a nail driven into the rocky substrate. Locations are not described or shown in this report because *C. robbinsorum* is included in the Federal list of threatened species and illegal commercial harvesting is a potential threat to this cactus.

Plants were censused on 5–6 April 1988, 11 April 1989, 13 April 1989, 17–18 April 1990, 22–23 April 1991, 5 May 1992, and 19–20 April 1993. Number of flowers, fruits and width of stem(s) were recorded for each individual. Width of stem was measured with a caliper. At the time of each inventory, flowering had recently ceased. The flowers had shriveled but their remains were still present. As a result, the number of flowers as well as the number of developing fruits produced could be counted. Precipitation data were obtained from a site within 1.5 km of the study site.

Matrix analysis. We recognized four stage-classes: seeds (S), juveniles ≤ 11 mm in diameter (J1), juveniles > 11 mm in diameter (J2), and adults (A). The seed stage-class includes seedlings less than 3 mm in diameter. No seedlings less than 3 mm in diameter were found during the censuses and, for the matrix analysis, can be included in the seed stage-class. Juveniles were divided into two stage-classes because the smaller plants experienced greater rates of mortality than did the larger juveniles.

The life cycle graph for *C. robbinsorum* (Fig. 1) is directed and stage-classified, rather than age-classified. An individual in stage class i may survive and grow to stage class $i + 1$ with probability G_i , or may survive and remain in stage class i with probability P_i .

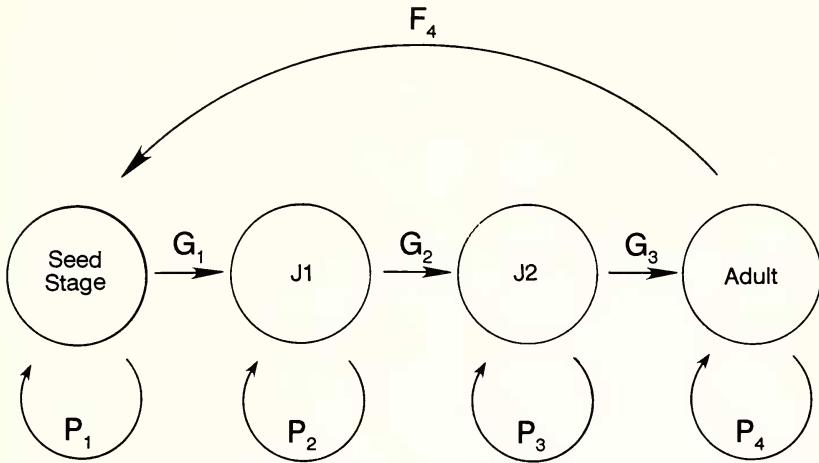


FIG. 1. Stage-classified life cycle used to depict the life cycle of *Coryphantha robbinsorum*. Stage 1 = seed stage; 2 = J1 stage; 3 = J2 stage; and 4 = adult stage. F_4 = fecundity (mean number of seeds produced per plant per year) of adults. G_i is the proportion of plants in the i th stage entering the next stage, G_{i+1} . P_i is the proportion of plants remaining and surviving in the i th stage.

The illustration also indicates that an individual may not shrink or skip a stage within a single time interval. However, some plants were observed to decrease in diameter between censuses. We treated the 14 cases (out of a total of 184 J2 observations) in which a J2 shrunk to a J1 size as remaining in J2. Plants were scored as adults if there was evidence of flowering in the season of the census or if the plant had flowered during earlier censuses; nonflowering adults were still adults.

For the matrix analyses, each plot was analyzed separately. The parameters p_i and g_i used in the matrix of a particular plot were the means obtained during the five years from that plot. There was one exception to using parameter values unique to the particular plot. The same value for adult fecundity, F_4 , was used for all of the matrix analyses (except when F_4 was specifically modified). Because (1) the mean number of fruits produced per adult per year, a , was determined to be 1.6 (for all adult plants, for all five years) and (2) the average number of seeds per fruit, b , was reported to be 20 (Zimmerman 1978), F_4 was estimated to be 33; $F_4 = ab$. To determine the effect that the particular choice of our F_4 estimate had on the matrix analysis, the analyses were run using a high value (80, when $b = 50$) and a low value (9.6, when $b = 6$) for F_4 . These high and low values are very likely to bracket the actual F_4 for individuals in this population. Hildegard Nase (personal communication 1993) has harvested 2000 seeds per year for two years from 40–45 greenhouse-

$$\begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

FIG. 2. Stage-classified projection matrix used in this analysis.

grown stems of *C. robbinsorum*, or about 44–50 seeds per stem per year. In developing the matrix, the choice of mean number of seeds per fruit affects not only fecundity, F_4 , but also G_1 , the proportion of seeds becoming J1.

We did not measure P_1 , the persistence of seeds in the seed bank. Steenberg and Lowe (1977) found that saguaros (*Carnegiea gigantea*) develop essentially no seed bank, largely due to seed predation. For the purposes of generating a very conservative analysis, we assumed that seeds remained in the seed bank for no more than one year; this assumption set P_1 at zero. We ran the general matrix analysis with P_1 set at zero, and also with P_1 set at 0.5 to determine the effect of a persistent, expanding seed bank on λ .

In order to examine the effects of changes in survival probabilities in selected life stages on λ , we altered the values for the survival probabilities of each stage, held the remaining matrix components constant, and simulated the population response. The survival probabilities in stages J1, J2 and A were modified by reducing the stage-specific annual survival by 50% and then calculating P_i and G_i using the equations of Crouse et al. (1987),

$$P_i = \frac{1 - p_i^{d-1}}{1 - p_i^d} p_i$$

and

$$G_i = \frac{p_i^d(1 - p_i)}{1 - p_i^d}$$

where d is the stage-specific mean age.

For analyzing the stage-structured transition matrix (Fig. 2), we used STAGECOACH, a program devised by Cochran and Ellner (1992).

RESULTS

Plant densities. Mean density between years of *C. robbinsorum* plants was the same on plots A and C (1.11 plants per meter² for all stages combined) (Table 1). Plot B had a lower density (0.70 plants per meter²). Significant between-year differences in numbers of individuals in all stages of Plot C were found. Also, the number

TABLE 1. NUMBER OF *C. ROBBINSORUM* PLANTS OF EACH STAGE-CLASS AND NUMBER OF FLOWERS (FL) AND FRUITS (FT) ON THE THREE STUDY PLOTS. Chi-square values of year to year variation in numbers of plants indicated as significant (*, $P < 0.005$) or not significant (NS, $P > 0.01$).

Plot	Stage	Year					Mean	P
		1989	1990	1991	1992	1993		
A	J1	23	34	29	20	22	25.6	NS
	J2	8	10	12	19	15	12.8	NS
	A	20	23	23	26	29	24.2	NS
	Fl	26	36	45	52	38	39.4	NS
	Ft	23	30	44	50	32	35.8	*
	total	51	67	64	65	66	62.6	NS
B	J1	8	6	7	5	4	6.0	NS
	J2	18	13	7	7	7	10.4	NS
	A	17	19	25	27	27	23.0	NS
	Fl	33	40	53	63	49	47.6	NS
	Ft	33	40	47	61	49	46.0	NS
	total	43	38	39	39	38	39.4	NS
C	J1	23	15	11	4	9	12.4	*
	J2	31	27	18	16	6	19.6	*
	A	14	23	34	41	43	31.0	*
	Fl	20	36	74	85	70	57.0	*
	Ft	18	29	59	76	63	49.0	*
	total	68	65	63	61	58	63.0	NS

of fruits in Plot A and flowers and fruits in Plot C varied significantly between years (Table 1).

Effect of rainfall on demographic parameters. The demographic parameters that were obtained from the yearly censuses of the three plots are presented in Table 2. Rainfall data are presented in Table 3. The period during the censuses included the driest seasons recorded for 12 years (the winter of 1989 and the summer of 1990).

Number of new J1 juveniles for all plots combined did not vary significantly among the four years ($\chi^2 = 9.73$, $P > 0.01$). Annual variation in the number of new J1 individuals was negatively correlated with total annual rainfall ($Y = 42.53 - 0.07X$, $r = -0.95$, $P < 0.01$), but was not significantly correlated with either summer ($P > 0.5$) or winter ($P > 0.5$) rainfall alone.

Percent mortality did not vary significantly among the four years for individuals in J1 ($\chi^2 = 2.2$, $P > 0.5$), J2 ($\chi^2 = 4.2$, $P > 0.1$), or A ($\chi^2 = 7.0$, $P > 0.05$) stages. However, percent survival of the J1 stage was positively correlated with winter rainfall ($Y = 70.43 + 0.05X$, $r = 0.98$, $P < 0.05$) and not significantly correlated with preceding annual ($P > 0.1$) or summer rainfall ($P > 0.5$). Percent mortality of the J2 stage was not correlated with rainfall. Percent

TABLE 2. DEMOGRAPHIC PARAMETERS OBTAINED FROM 5 CENSUSES OF THREE PERMANENT PLOTS OF *C. ROBBINSORUM* IN SOUTHEASTERN ARIZONA.

	Year				Mean
	1990	1991	1992	1993	
Number of New Individuals on Plot					
Plot A	15	10	6	3	8.5
Plot B	2	4	1	2	2.3
Plot C	5	6	2	4	4.3
Total	22	20	9	9	15.0
Mortality (pooled data from the 3 plots)					
J1	0.264	0.204	0.170	0.200	0.209
J2	0.036	0.082	0.026	0.073	0.054
A	0.037	0.000	0.013	0.056	0.027
Plot A Transition Matrix Elements					
P ₂	0.783	0.625	0.517	0.762	0.672
P ₃	0.900	0.900	0.846	0.750	0.849
P ₄	1.000	0.957	1.000	0.920	0.969
G ₁	0.042	0.017	0.007	0.003	0.017
G ₂	0.087	0.156	0.345	0.143	0.183
G ₃	0.100	0.100	0.154	0.200	0.138
Plot B Transition Matrix Elements					
P ₂	0.333	0.667	0.571	0.400	0.493
P ₃	0.750	0.460	0.857	0.857	0.731
P ₄	0.941	1.000	1.000	1.000	0.985
G ₁	0.003	0.005	0.001	0.002	0.003
G ₂	0.222	0.000	0.286	0.000	0.127
G ₃	0.188	0.460	0.143	0.143	0.234
Plot C Transition Matrix Elements					
P ₂	0.380	0.375	0.182	0.800	0.434
P ₃	0.700	0.500	0.667	0.571	0.610
P ₄	0.933	1.000	0.971	0.921	0.956
G ₁	0.014	0.010	0.002	0.003	0.007
G ₂	0.286	0.500	0.545	0.000	0.333
G ₃	0.267	0.385	0.278	0.286	0.304

mortality of the adult stage was positively but not significantly correlated with summer rainfall ($Y = 0.07X - 11.76$, $r = 0.90$, $P < 0.2$).

The number of flowers (all plots combined) and the number of fruits (all plots combined) were not significantly correlated with the amount of rainfall (for summer, winter or total) during the preceding year. The number of flowers ($Y = 49.97 + 0.44X$, $r = 0.72$) and the number of fruits ($Y = 60.86 + 0.46X$, $r = 0.68$) produced in all plots combined were weakly correlated with the amount of winter precipitation ($P < 0.2$ for both).

Growth and reproduction. Growth was determined as the change in plant diameter from one census to the next. There was a significant

TABLE 3. RAINFALL (mm) AT A SITE WITHIN 1.5 KM OF THE *CORYPHANTHA ROBBINSORUM* POPULATION IN COCHISE COUNTY, ARIZONA. Rainfall data are divided into summer (May through September) and winter (October through April of the following year). Means based on data from 1981 to 1992.

Year	Summer	Winter	Total
1988	367	168	535
1989	196	65	261
1990	155	199	354
1991	197	250	447
1992	229	227	456
1993	235	—	—
12 yr mean	260 ± 90	233 ± 127	493 ± 177

negative relationship between plant diameter and growth for three of the four between-year transitions (Table 4). Small plants increased in diameter at a greater rate than large plants. The negative relationships were not simply a result of using a linear dimension (plant diameter) to measure growth (which is three dimensional). For three of the years, half of the plants over 2 cm in diameter either did not grow or decreased in diameter (Table 5). After the 1992 census, 68% of the plants over 2 cm in diameter shrank or at least did not grow. Based on the linear regressions in Table 4, a plant was likely to shrink from one year to the next if its diameter exceeded 31.2 mm in 1990, 28.1 mm in 1991, and 20.0 mm in 1992. There was a modest, but not significant, correlation between the amount of winter precipitation occurring between two censuses (X ; Table 3) and the slopes of the linear regressions (Y ; Table 4) for the four between-year transitions ($Y = 0.47X - 14.81$, $r = 0.86$, $P = 0.1$) (r = correlation coefficient).

The percentage of *C. robbinsorum* plants that produced flowers and fruits increased with plant diameter (Fig. 3). The smallest plants that flowered (and fruited) were 13 mm in diameter. At 18 mm, over half of the plants both flowered and fruited. Of the plants ≥ 25 mm in diameter, over 94% flowered and 75% fruited. Large adults produced more flowers and fruits than did small adults (Fig. 4). Over

TABLE 4. LINEAR REGRESSIONS OF Y , CHANGE IN PLANT DIAMETER (cm) AFTER ONE YEAR ($t_0 + 1$), IN RELATION TO X , PLANT DIAMETER (cm) OF PRECEDING YEAR (t_0). $Y = a + bX$.

Year (t_0)	N	Slope (b)	Y-intercept (a)	P > F	X, when Y = 0
1989	142	-0.020	0.128	0.4275	6.35
1990	150	-0.076	0.239	0.0015	3.12
1991	155	-0.130	0.364	0.0001	2.81
1992	153	-0.063	0.128	0.0097	2.02

TABLE 5. NUMBER (AND PROPORTION) OF *CORYPHANTHA ROBBINSORUM* PLANTS GROWING OR NOT GROWING BETWEEN YEARS.

	Year (t ₀)			
	1989	1990	1991	1992
Plants ≥ 2 cm				
Growing	24 (.53)	26 (.48)	33 (.53)	23 (.32)
Shrinking or not growing	21 (.47)	28 (.52)	29 (.47)	48 (.68)
Plants < 2 cm				
Growing	62 (.64)	67 (.70)	78 (.84)	38 (.46)
Shrinking or not growing	35 (.36)	29 (.30)	15 (.16)	44 (.54)
Total shrinking or not growing	56 (.39)	57 (.38)	44 (.28)	92 (.60)
Total	142	150	155	153

50% of all of the fruit produced during the five years by this population were from 25 individuals that represented only 23% of the adult population.

About 7.2% of the flowers did not set fruit. The flowers on small plants were more likely to set fruit than the flowers on large plants. When 4 categories of plant sizes (13–17, 18–22, 23–27 and 28–35 mm) were examined using a χ^2 test of homogeneity, the category of largest plants had a disproportionately greater frequency of flowers failing to set fruit ($\chi^2 = 11.2$, $0.025 < P < 0.01$) (Table 6). Plants with clusters of five or more flowers were also more likely to include flowers that did not set fruit when compared to plants with clusters of 1, 2, 3, or 4 flowers ($\chi^2 = 18.1$, $P < 0.001$) (Table 7).

Matrix analyses. The results of the matrix analyses are given in Table 8. For each plot, λ is greater than 1.0, indicating that the populations are growing. From the projection analysis, the population generation time, \bar{A} , is determined to be 16.9 years for Plot A, 60.7 years for Plot B and 17.3 years for Plot C.

The unrealistically large \bar{A} value calculated for Plot B must result from P_4 , G_1 , or G_2 , since these were the only parameters differing from their counterparts in Plots A and C. For Plot B, P_4 was greater

TABLE 6. THE NUMBER OF FLOWERS DEVELOPING INTO FRUITS IN RELATION TO PLANT DIAMETER. Data based on all years and all plots.

Number of flowers	Diameter of plant (cm)			
	1.3–1.7	1.8–2.2	2.3–2.7	2.8–3.5
Set fruit	46	217	205	189
Did not set fruit	2	11	12	26
Total	48	228	217	215

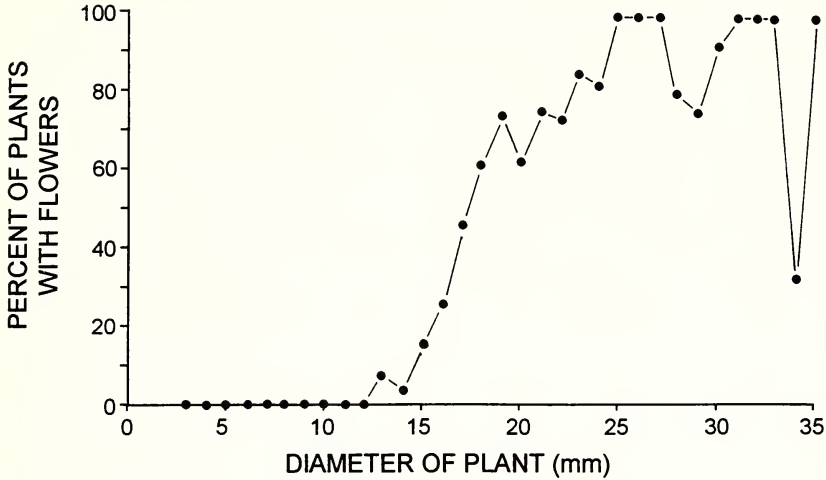


FIG. 3. Flower production by *C. robbinsorum* measured as the proportion of flower-bearing plants in 1 mm diameter increments. Data were collected in 1989–1993 from all plants within Plots A, B, and C. Data within each diameter class are pooled over five years.

while G_1 and G_2 were less than the same parameters for the other plots. When each of these parameters was adjusted so that it was within the range of values for Plots A and C, matrix analyses were performed changing a single parameter at a time. The effects of each of the three parameter changes on \bar{A} (Table 9) suggests that the lower than usual values of G_2 and especially G_1 had the greatest effect on \bar{A} . Reducing the P_4 value of Plot B to one that was more like the other plots had only a modest effect on \bar{A} . When fecundity, F_4 , was increased to 80 or reduced to 9.6 and the matrices reanalyzed, there was no appreciable effect on either λ or \bar{A} for any of the plots (Table 9).

For Plot C, the simulated 50% reduction in survivorship of each of the four stage-classes resulted in only a modest decrease in λ (but with λ still > 1) for seeds (to juveniles) (Table 9). Reducing the survivorship of J1 or J2 produced an intermediate effect on λ . If a stable age distribution could be (but can not be) obtained for the case of a 50% reduction in the survivorship of either J1 or J2, the predicted \bar{A} values would be 451 years for J1's and 67,000 years for J2's. A 50% reduction in survival of the adult stage-class produced the greatest change in λ ; λ fell from +1 to 0.82.

For Plot C, simulations were made of the effect of increasing survivorship for each stage-class (Table 9). A modest increase in λ is seen when seed bank survival (P_1) is increased from 0 to 0.5. A profound increase in λ is noted when any other P value is raised to 1.0.

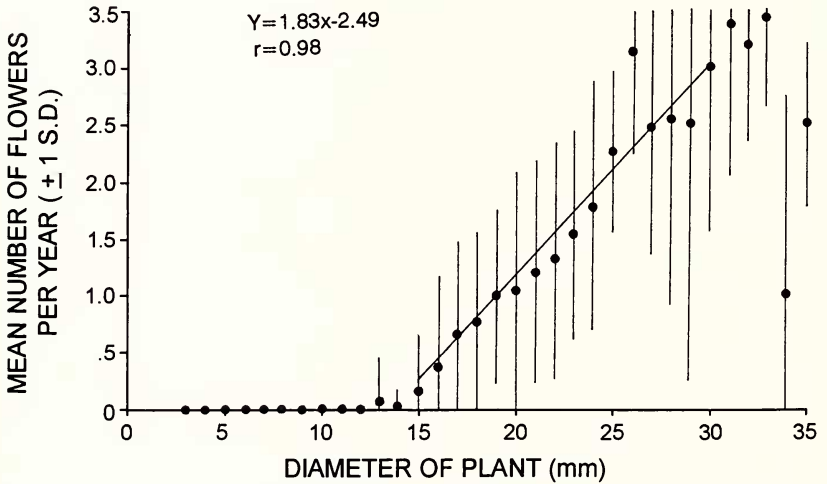
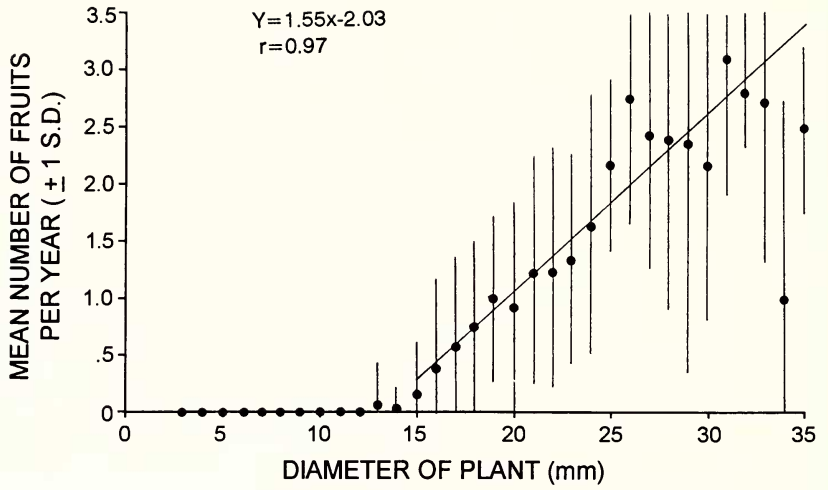


FIG. 4. Relationship between plant diameter and number of flowers and fruits produced by individuals of *C. robbinsorum*, Cochise County, Arizona. Mean production of flowers and fruits based on all individuals (regardless of their stage) in each size class. Vertical bars = one standard deviation.

TABLE 7. THE NUMBER OF PLANTS WITH ALL FLOWERS PRODUCED IN A YEAR SETTING FRUIT OR ONE OR MORE OF THE FLOWERS NOT SETTING FRUIT. Data based on all years and all plots.

Number of plants	Number of flowers produced per season				
	1	2	3	4	5-7
All flowers set	119	102	55	18	6
1 or more flowers not set	9	12	6	7	4

DISCUSSION

Effect of rainfall on demographic parameters. *Coryphantha robbinsorum* had several unanticipated responses to rainfall regimes. Increased rainfall was expected to increase survivorship, especially for the smallest size-class. However, the *only* stage-class that appeared to benefit from increased rain was J1; J1 survivorship increased with increasing winter rainfall. Previous studies of cacti have shown that survival of the youngest stage-classes increases with increased rainfall (Johnson et al. 1993; Steenbergh and Lowe 1969). Increased annual rainfall appeared to *decrease* the number of new J1's to the population. There also appeared to be a modest increase in the mortality of adults after summers with more rainfall.

Although the causes of mortality of *C. robbinsorum* were not determined in this study, several factors should be considered. The plants occur in the cracks of limestone outcrops, in well-drained microsites (U.S. Fish and Wildlife Service 1993). Another cactus, *Carnegiea gigantea*, is restricted to natural rock piles in the southern portion of its range (Steenbergh and Lowe 1977, p. 118). The rock piles are thought to afford well-drained sites in an area (extreme southern Sonora, Mexico) that often has saturated soils after hot summer rains. Hot humid conditions increase the susceptibility of cactus plants to lethal infestations of fungi (Booth and Alcorn 1959; Gene Joseph personal communication 1993). In the same context, four cacti that occur on gravel or well-drained limestone outcrops in southern Arizona, *C. robbinsorum*, *Echinocereus fendleri*, *E. pectinatus* var. *rigidissimus*, and *Neolloydia intertexta*, when grown

TABLE 8. THE RESULTS OF MATRIX ANALYSIS OF DEMOGRAPHIC DATA FROM THREE *C. ROBBINSORUM* MONITORING PLOTS. Data pooled for all years for each plot. Ages are expressed in years.

	λ	Mean age as seed	Mean age as J1	Mean age as J2	Mean age as adult	Population generation time
Plot A	1.094	1.000	2.031	4.425	9.343	16.799
Plot B	1.003	1.000	1.378	3.431	53.655	60.695
Plot C	1.041	1.000	1.107	5.125	17.301	17.301

TABLE 9. SENSITIVITY ANALYSIS OF *C. ROBBINSORUM* POPULATIONS. Resultant λ and \bar{A} , 'baseline runs' and after (1) simulated adjustment of three parameters for the matrix of Plot B so that these parameters resemble the same parameters of Plots A and C, (2) simulated change in fecundity from a baseline of 33 seeds per plant per year to 80 seeds and to 9.6 seeds (3) simulated 50% decrease in survival probabilities of parameters for Plot C, and (4) simulated increase in survival probabilities of parameters for Plot C.

Stage parameter	Change in initial matrix		Result	
	Old	New	λ	\bar{A}
Adjustment of Plot B Parameters				
	baseline run		1.003	60.695
P ₄	.985	9.60	.982	52.413
G ₁	.003	.010	1.041	25.009
G ₂	.127	.250	1.018	37.124
Change in Fecundity				
Plot A				
F ₄ = 33	.017	—	1.094	16.799
F ₄ = 80	.017	.006	1.083	17.741
F ₄ = 9.6	.017	.037	1.067	19.546
Plot B				
F ₄ = 33	.003	—	1.004	60.695
F ₄ = 80	.003	.001	1.004	60.398
F ₄ = 9.6	.003	.009	1.003	61.539
Plot C				
F ₄ = 33	.007	—	1.042	17.301
F ₄ = 80	.007	.003	1.041	17.351
F ₄ = 9.6	.007	.023	1.0378	17.825
50% Decrease in Plot C Parameters				
	baseline run		1.041	17.301
G ₁	.007	.004	1.007	25.042
P ₂	.434	.204	.958	451.420
G ₂	.333	.008		
P ₃	.609	.303	.956	67,487.000
G ₃	.304	<.001		
P ₄	.956	.478	.822	9.371
Increase in Plot C Parameters				
P ₁	.000	.500	1.085	14.209
P ₁	.000	1.000	12.048	14.312
P ₂	.434	1.000	11.685	15.525
P ₃	.609	1.000	11.483	16.324
P ₄	.956	1.000	10.734	19.610

commercially are more likely to die than other cactus species after rains or irrigation during late summer and early fall (Gene Joseph personal communication 1993).

Coryphantha robbinsorum flower buds develop on the previous year's growth (Hildegard Nase personal communication 1993). Although reproductive output responds to increased rainfall for other

cacti (Johnson et al. 1993; Steenberg and Lowe 1983), there was only a weak correlation between amount of winter rainfall and number of flowers and fruits produced by the entire study population.

Growth and reproduction. There are two unusual features of *Coryphantha robbinsorum* growth. The first is that, while most juveniles increased in diameter from year to year, about half of the adults over 2 cm in diameter either did not change or decreased in diameter between years. The other feature is that there was a greater tendency of plants to shrink from one year to the next with wetter intervening winters. *Coryphantha robbinsorum* in the wild may be as susceptible to root rot in winter as cultivated populations of cacti.

Plants did not begin to reproduce until they were at least 13 mm in diameter. The relationship between increasing plant size and the probability of flowering for *C. robbinsorum* resembles that of *Echinomastus erectocentrus* var. *acunensis* (Johnson et al. 1993). Large adults (≥ 25 mm diameter) were more likely to flower than small adults and, because they also were more likely to have more flowers and fruits per individual than small individuals, contributed a disproportionate number of fruit to the population.

Steenbergh and Lowe (1977) demonstrated experimentally that 50% of the potential stem growth per year of small (4–5 m height) *Carnegiea gigantea* individuals is diverted into its yearly reproductive effort. If the reproductive investment were similar for small *C. robbinsorum*, small adult plants might be more resource-limited than large adults during reproductive bouts and more likely to respond to this limitation by aborting ripening fruit more frequently than adults. Flowers produced by the largest adults (2.8–3.5 mm) were more likely to abort than flowers produced by any other flowering size-class. Plants with large flower clusters (≥ 5 flowers per plant) were more likely to include flowers that failed to set fruit than plants with single flowers or smaller clusters. A single flower of *C. robbinsorum* reopens each day for about seven days (Hildegard Nase personal communication 1993). We do not know if the number of flowers per cluster affects pollinator movement nor what other factors may be responsible for the reduced fruit set of larger adults.

Matrix analysis. Several important attributes of the population and of the characteristic life history of *Coryphantha robbinsorum* become available with matrix analysis. One attribute of the population, λ , is greater than 1.0 for each of the plots. A λ greater than 1.0 indicates that the population is currently expanding in each of these plots. The mean λ for the three plots, 1.0464, predicts a doubling time for the population of about 16 years. The λ values of the three plots are very similar. Comparison with other published values of λ (Burns and Ogden 1985; Pinerio et al. 1984; Caswell 1986)

suggests that *C. robbinsorum* has a finite rate of population increase more similar to that measured for the large understory palm, *Astrocaryum*, and both tropical and temperate tree species than that measured for most herbaceous plants.

The behavior of the populations of small dense patches of *C. robbinsorum* needs to be examined over a longer time period. Since the known populations of this cactus are nowhere both dense and extensive, the measured value of λ is expected to decrease over time in these study plots. When λ decreases, appropriate monitoring of the populations may detect if density-dependent mortality factors are regulating population size.

Zimmerman (1985 and personal communication 1993) has hypothesized that predation (or parasitism) may be one factor regulating the densities and distribution patterns of *Coryphantha robbinsorum* populations. Zimmerman has found *C. robbinsorum* plants freshly killed by a cerambycid beetle (*Moneilema corrugans*), a cactus weevil (*Gerstaeckeria* sp.) and a *Yosemitia* sp. moth. The larvae of these insects feed on the internal tissues and can kill adult plants, particularly by damaging the xylem. However, the causes of mortality in relation to population density remain unexplored for *C. robbinsorum*.

Sensitivity and elasticity analyses performed on these matrices demonstrated that the value of λ in these three plots was largely dependent on the survival (P_4) of the adult population. Altering fecundity or seedling establishment has little effect on λ in these three plots. Management schemes to safeguard populations of *C. robbinsorum* should focus on protection of adult plants. A management scheme that focuses on adult plants would be similar to that recommended by Crouse et al. (1987) for the Atlantic populations of loggerhead sea turtles (*Caretta caretta*). P_i and G_i values of the late juveniles and adults for both populations have the greatest effect on λ .

This study is the first one to estimate the population generation time, \bar{A} (=mean age of parents contributing seed to the next generation at a stable age distribution), of any cactus. The value of \bar{A} obtained for Plots A and C suggest that the average adult age in situ is about 17 years. However, most species of small cacti appear to reach adulthood much sooner in horticulture than in situ. With the enhanced growing conditions in cultivation, some individuals of *C. robbinsorum* flower in their second year and most in their third year (Gene Joseph personal communication 1993; Hildegard Nase personal communication 1993). One small cactus that requires a long time to mature in cultivation is *Echinocactus horizonthalonius* var. *nicholi*. Mark Dimmitt (personal communication 1993) has found that this plant requires at least 10 years to flower from seed in

cultivation and estimates that individuals in nature may require at least 30 years to mature.

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ANNOUNCEMENT

THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Ing. Nelson Zamora, of the Instituto Nacional de Biodiversidad (INBio), Costa Rica, is the recipient of the **1994 Rupert Barneby Award**. Ing. Zamora will be working on several groups of Mimosoid and Caesalpinoid Legumes for Costa Rica.

The New York Botanical Garden also invites applications for the **1995 Rupert Barneby Award**. The award of \$1,000.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1996 and January 31, 1997. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126 USA, and received no later than December 1, 1995. Announcement of the recipient will be made by December 15th. Anyone interested in making a contribution to **THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS**, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.